
INVASIVE ANTS: UNWANTED PARTNERS IN ANT-PLANT INTERACTIONS?¹

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ABSTRACT

As invasive ants spread, their interactions with plants are inevitable and have potentially great implications for agriculture and conservation. When considered in the context of pre-existing models of ant-plant interactions, the higher abundance, aggressive nature, and attraction to high-carbohydrate resources typically associated with invasive ants lead to hypotheses about how invasive ants may differ from native ants in protecting plants from herbivores, tending of Homoptera, and interactions affecting plant reproduction. Examples demonstrate that all three of these traits common to invasive ants can influence the outcome of interactions between invasive ants and plants, but ant biology and attributes of other organisms also determine the consequences for the plant. Drawing from these examples and considering traits of the invasive ants, plants, and other organisms that interact with the plant, I offer predictions for the contexts in which plants will be at high and low risk of adverse outcomes or may benefit from interacting with an invasive ant. The potential for effects of invasive ants on plants to counteract, and the complexity and context-dependency that are hallmarks of ant-plant interactions generally, preclude drawing simple conclusions about the net impacts of invasive ants on plants. Further research on interactions between invasive ants and plants will contribute directly to conservation and agriculture, and provide insights to invasion ecology and our understanding of ant-plant interactions.

Key words: abundance, aggression, byproduct mutualism, carbohydrates, context-dependent outcomes, extrafloral nectaries, Homoptera, invasive ants.

Interactions between ants and plants range from facultative, loose associations to species-specific, obligate mutualisms, and innumerable questions have been posed about the costs, benefits, and evolutionary implications of these relationships (Beattie, 1985; Bronstein, 1994; Jolivet, 1996). As invasive ants spread, their interactions with plants are inevitable and have potentially great implications for agriculture and conservation. To what extent are ant-plant interactions altered by the introduction of these novel partners?

Invasive ants possess a distinct combination of traits relative to native ants (Holway et al., 2002). In this paper, I hypothesize that some of these traits will affect how invasive ants associate with plants and provide a basis for predicting the outcome of these novel interactions. I focus on the potential for differences between native and invasive ants in the way they protect plants from herbivory, tend Homoptera, and interfere with plant reproduction. These examples encompass the more facultative, ubiquitous interactions in which invasive ants are increasingly likely to participate as they spread around the globe.

Although I explore the differences between na-

tive and invasive ants for each type of interaction separately, the same ant can interact directly and indirectly with the same plant in multiple ways. Invasive ants that benefit the plant in one interaction may be detrimental to the plant in another. The net outcome for the plant will depend on the relative balance of a range of interactions, all of which in turn will be influenced by the same set of variables that typically influence ant-plant interactions. Ultimately, we will want to know whether invasive ants have the ability to tip the balance of interactions toward consistently positive or negative outcomes for the plants, and how these outcomes can be manipulated to achieve land management goals.

INVASIVE ANTS

Of the approximately 10,000 species of ants in the world, about 150 have been introduced around the world with the help of humans; these may be termed exotic, or tramp ants (McGlynn, 1999). Invasive ants are the small subset of introduced ants that are able to establish and penetrate areas outside of human-modified habitats (Holway et al., 2002). Well-known examples in the United States include the red imported fire ant, *Solenopsis invicta*,

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and the Argentine ant, *Linepithema humile*. The little fire ant, *Wasmannia auropunctata*, the big-headed ant, *Pheidole megacephala*, and long-legged ant, *Anoplolepis gracilipes*, also appear to be highly successful invaders, although they are far less studied. See Table 1 for a summary of distributions.

One hallmark of invasive ants is their ability to become extremely abundant in their new habitats. Pitfall traps in areas invaded by *Solenopsis invicta* (Porter & Savignano, 1990), *Linepithema humile* (Holway, 1998), and *Pheidole megacephala* (Hoffman et al., 1999) have all shown that the number of invasive ant workers greatly exceeds that of native ants in nearby un-invaded areas. Several mechanisms are likely contributing to invasive ants' achievement of numerical superiority including escape from natural enemies and competitors and changes in colony structure toward multi-queened, multi-nest supercolonies that lack intraspecific aggression (Holway et al., 2002).

The physiology and behavior of invasive ants also likely play a role in their tendency to achieve high abundance (Holway et al., 2002). Ecologically dominant ants, including invasive ants such as *Linepithema humile*, have modified crops that allow them to take in more liquid foods, including floral and extrafloral nectar and homopteran honeydew (Eisner, 1957; Davidson, 1998). The ability to harvest these carbohydrate-rich resources may be especially important in fueling the high tempo activity of a large workforce, thereby maintaining a high dynamic density (ants/area/time) (Tennant & Porter, 1991; Davidson, 1997; Davidson, 1998). Individual nests can be highly vagile, allowing invasive ants to move in response to the availability of resources (Passera, 1994). Even *Solenopsis invicta*, which nests in mounds, will create satellite nests at the base of plants when tending aphids (Kaakeh & Dutcher, 1992). A high level of aggression is another character common to invasive ants and likely enhances their success as predators (Holway et al., 2002). Access to prey and carbohydrate-rich resources and a large workforce are both the cause and effect of superior exploitative and interference competition abilities through which native ants and other competitors may be displaced (Holway et al., 2002).

Displacement of native ants is the most commonly documented consequence of an invasive ant introduction (Holway et al., 2002). *Linepithema humile*, for example, has displaced several species of epigaeic ants in California (Erickson, 1971; Ward, 1987; Holway, 1995; Human & Gordon, 1996), Portugal (Cammell et al., 1996; Way et al., 1997), and South Africa (Donnelly & Giliomee, 1985). *Wasmannia auropunctata* has expanded its territory

Table 1. Native and introduced ranges of some invasive ants.

Species	Common name	Native range	Introduced range	References
<i>Anoplolepis gracilipes</i> (F. Smith)	long-legged or crazy ant	in dispute	Asia, Australia, Pacific and Indian Ocean islands	Fluker & Beardsley (1970), Haines & Haines (1978), Veeresh & Gubbaiah (1984), Fellowes (1999), Green et al. (1999), Young et al. (2001)
<i>Linepithema humile</i> (Mayr)	Argentine ant	Argentina and Brazil	Mediterranean-type climates of all continents, Hawai'i, Bermuda	Haskins & Haskins (1965), Fluker & Beardsley (1970), Majer (1994), Suarez et al. (2001)
<i>Pheidole megacephala</i> (Fabricius)	big-headed ant	tropical Africa	South America, Asia, Australia, U.S., Pacific Ocean islands, Bermuda	Haskins & Haskins (1965), Greenslade (1971), Room (1975), Fluker & Beardsley (1970), Majer (1985), Fowler et al. (1990), Fellowes (1999), Deyrup et al. (2000)
<i>Solenopsis invicta</i> (Buren)	red imported fire ant	Brazil	U.S., Australia	Vinson & Greenberg (1986), Holway et al. (2002)
<i>Wasmannia auropunctata</i> (Rogers)	little fire ant	neotropics	Africa, continental U.S., Hawai'i, Galapagos Islands, New Caledonia	Spencer (1941), Entwistle (1972), Fabres & Brown (1978), Williams (1994), Conant & Hirayama (2000)

at the expense of native ants on the Galapagos Islands (Lubin, 1984). *Pheidole megacephala* has diminished the native ant populations of several habitats in Australia (Majer, 1985; May & Heterick, 2000; Hoffman et al., 1999; Vanderwoude et al., 2000). *Solenopsis geminata* (F.) and other ants native to the southern U.S. have become much less common following invasion by *S. invicta* (Porter & Savignano, 1990; Gotelli & Arnett, 2000).

Invasive ants also affect other invertebrates and even vertebrates, usually negatively. *Anoplolepis gracilipes* is blamed for diminished populations of various invertebrates in the Seychelles (Haines & Haines, 1978) and is generating ecosystem-level changes through its impact on the red land crab on Christmas Island (Green et al., 1999). *Linepithema humile* is associated with decreases in some insects in California and Hawai'i (Cole et al., 1992; Bolger et al., 2000). The great reduction in endemic insects in lowland Hawai'i at the end of the 1800s has been attributed to invasion by *Pheidole megacephala* (Zimmerman, 1970). *Solenopsis invicta* has been linked to declines in a number of terrestrial invertebrates, birds, and mammals in the southern United States (Holway et al., 2002). *Wasmannia auropunctata* has eliminated or reduced terrestrial invertebrate populations in the Galapagos Islands (Lubin, 1984) and New Caledonia (Jourdan, 1997). The mechanisms for these effects are not always clear but likely involve some combination of predation and competition, via direct or indirect interactions (Holway et al., 2002).

PREDICTING THE NATURE AND OUTCOMES OF INVASIVE ANT-PLANT INTERACTIONS

A wealth of studies has established that the nature of ant-plant interactions is dependent on many variables including ant behavior, ant colony size and stage, host plant attributes, and the abundance and behavior of other organisms in the system (Buckley, 1982; Beattie, 1985; Keeler, 1989; Cushman, 1991; Davidson & McKey, 1993; Bronstein, 1994, 1998; Jolivet, 1996). As explained above, invasive ants tend to have larger colonies and exhibit more aggressive behavior than native ants. Moreover, invasive ants appear to have a stronger predilection than many native ants for carbohydrate resources, which are invariably obtained directly or indirectly from plants. Since native ants are frequently displaced when invasive ants enter a new habitat, it will be traits of the invaders that influence future outcomes for the plants. Applying existing models of ant-plant interactions, I develop hypotheses about how invasive ants' elevated abun-

dance, aggression, and affinity for carbohydrate-rich food affect how they might protect plants from herbivores, tend Homoptera, and interfere with plant reproduction.

ANT PROTECTION FROM HERBIVORES

Protection of plants from herbivores is perhaps the oldest recognized effect of ants on plants. As long ago as A.D. 304, Chinese citrus growers facilitated the spread of the yellow citrus ant, which preyed on herbivores in their orange orchards (Huang & Yang, 1987). Since then, ants' ability to prey on, or simply harass, would-be herbivores has been noted in many systems (Beattie, 1985; Hölldobler & Wilson, 1990). In some cases, plants entice ants by offering food or shelter. For example, it is thought that one of the primary reasons for the presence of extrafloral nectaries is to attract ants in exchange for protection from herbivores (Bentley, 1977).

A number of traits associated with invasive ants have been linked to plant defense: large colony size, high levels of worker activity, and aggressiveness (Davidson & McKey, 1993; Bronstein, 1998). A large number of very active workers may result in increased plant visitation by ants leading to decreased herbivory (Gaume et al., 1997; Bronstein, 1998; Gaume et al., 1998; Linsenmair et al., 2001) because herbivores are located more rapidly and have a shorter residence time on the plant (Duarte Rocha & Godoy Bergallo, 1992). Benefits to the plant probably level off or even decline at some colony size, however. An extremely large colony may impose a cost on the plant if the ants are stealing floral nectar, tending Homoptera, interfering with the natural enemies of herbivores, or excavating the plant's root system. Research to determine where the cost-benefit trade-offs lie with respect to ant colony size has yet to be done.

Aggressive behavior also aids in protecting the plant from herbivores (Fiala et al., 1989; Letourneau, 1983; Bronstein, 1998). Bentley (1977) related ant aggression on plants to three factors: predatory behavior, ownership behavior or the defense of territorial boundaries (Way, 1963), and swarming behavior or the ability to rapidly recruit workers. All three behaviors may be enhanced at the colony level by having a large workforce. Aggression is also negatively correlated with proximity to an ants' nest; disturbance near an ants' nest or food source will elicit a stronger response than a threat encountered farther away (Way, 1963). The vagile, polydomous nesting behavior of invasive ants may allow them to nest in closer proximity than a native

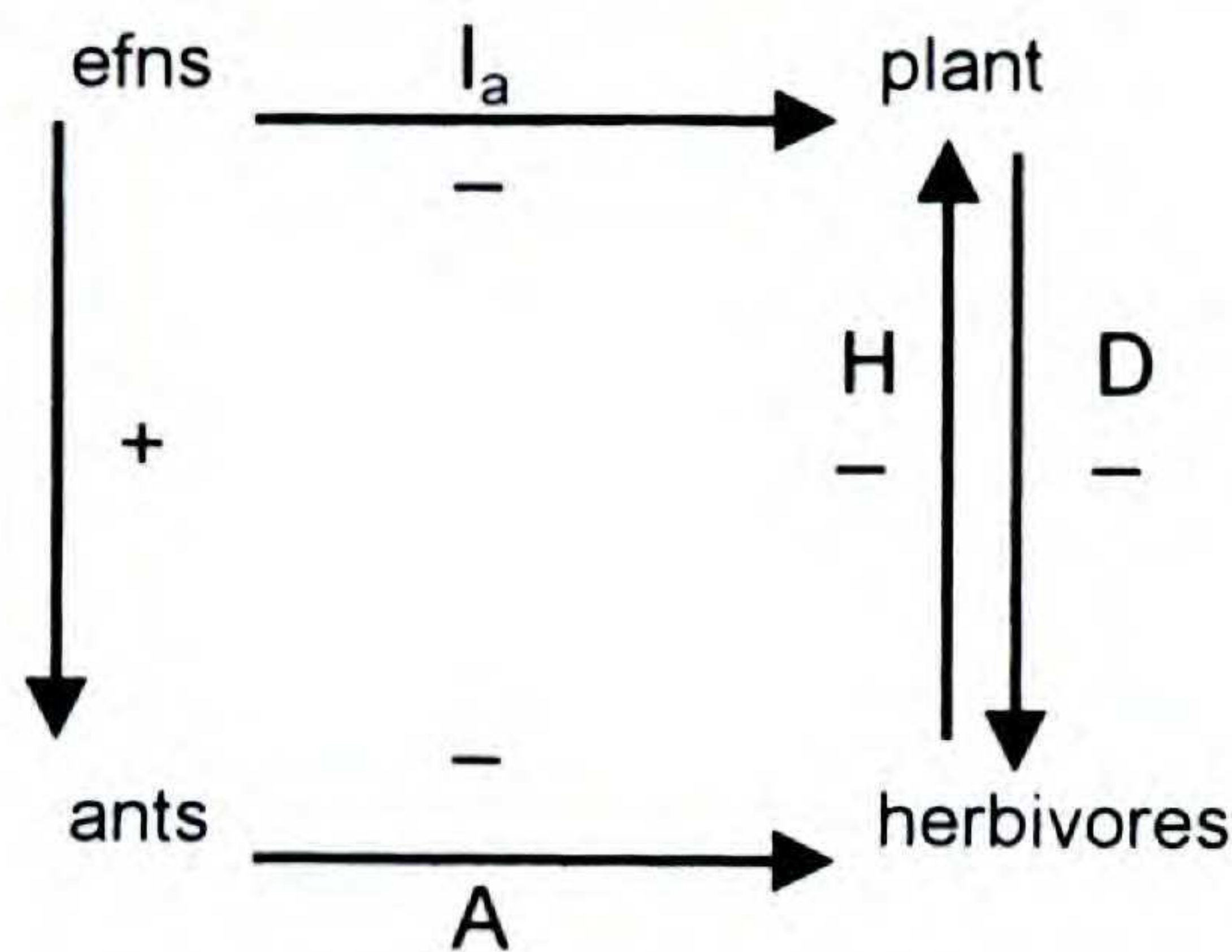


Figure 1. A schematic of the food-for-protection mutualism between ants and extrafloral nectaries. The extrafloral nectaries provide ants with food and the ants deter herbivores. The direction of the arrows indicates the direction of the effect and the positive and negative signs show the type of effect. A = effectiveness of ant-defense, D = effectiveness of other defenses, H = intensity of herbivory, I_a = investment in nectar and nectaries, and $efns$ = extrafloral nectaries.

ant would, possibly facilitating a greater aggressive response.

Some ants provide protection from herbivores while collecting extrafloral nectar. Keeler (1981: 490) modeled the conditions under which the mutualism is favored:

$$p[A(1 - D)H] > I_a$$

where p = probability that ants will find the plant, A = effectiveness of ant-defense, D = effectiveness of other defenses, H = intensity of herbivory, and I_a = investment in nectar and nectaries. From the plants' perspective, the mutualism is maintained when the left side of the equation, the benefits to the plant, exceeds the right side, the costs of attracting the ants (Keeler, 1981). A schematic of the relationship is shown in Figure 1.

Given the numerical superiority, attraction to carbohydrate resources, and aggressive character of invasive ants, we might expect that $p_{invasive} > p_{native}$ and $A_{invasive} > A_{native}$. Since D is primarily a factor of the plant and the herbivore(s), $D_{invasive}$ and D_{native} are not likely to differ. $H_{invasive}$ may exceed H_{native} if intraguild predation is a factor, i.e., if ants prey on or interfere with the natural enemies of herbivores (Eubanks, 2001). However, $H_{invasive}$ may be less than H_{native} if invasive ants diminish herbivore populations via direct or indirect interactions that affect herbivore eggs, larvae, pupae, or adults away from the plant. If extrafloral nectar production is an inducible defense (Koptur, 1989; Ness, 2001) I_a will increase with H . For example, if H_{native} is greater than $H_{invasive}$, then extrafloral nectaries will be induced more often when native ants are present, and $I_{a\ native}$ will be greater than $I_{a\ invasive}$.

If on balance, the left side of the equation increases and I_a stays the same, then there will be a greater benefit margin for the plant when invasive ants are present. If, however, the presence of invasive ants lowers the left side of the equation, then to maintain the mutualism, $I_{a\ invasive}$ may also need to be less than $I_{a\ native}$. For invasive ants that are aggressive, abundant, and attracted to carbohydrate-rich resources, the model predicts maintenance of the mutualism if the potential for herbivory is not diminished (e.g., through interactions away from the plant).

ANT TENDING OF HOMOPTERA

Ant tending of honeydew-producing Homoptera, including scale, mealybugs, aphids, and membracids, is a common indirect ant-plant interaction (Way, 1963; Carroll & Janzen, 1973; Buckley, 1987; Hölldobler & Wilson, 1990; Davidson & McKey, 1993). Homoptera extract phloem from the host plants and excrete it as honeydew. Ants feeding on the honeydew often protect these Homoptera from parasites and predators (Way, 1963; Buckley, 1987). The ant-Homoptera mutualism may be detrimental for the plant, robbing it of phloem and sometimes leading to mold accumulation (Bach, 1991; Lewis et al., 1976) or phytopathogen transmission (e.g., pineapple mealybug wilt disease (Beardsley et al., 1982), *Phytophthora* pod rot (Evans, 1973), swollen shoot virus (Taylor & Adeyoin, 1978)) while conferring no benefits in exchange (Buckley, 1987). Less commonly, the interaction may benefit the plant if ants deter other herbivores while tending Homoptera (Carroll & Janzen, 1973; Messina, 1981; Compton & Robertson, 1988).

As with plant protection from herbivores, the characters common to many invasive ants will affect their Homoptera-tending abilities and consequently the outcome for the plant. The need for carbohydrate resources and ability to harvest copious amounts of liquid provides the basis for the attraction of invasive ants to Homoptera. Ant aggression, particularly ownership behavior, is an effective deterrent to most would-be parasites and predators of Homoptera (Way, 1963). Polydomy and nest vagility may allow invasive ants to reside in closer proximity to these carbohydrate resources than would native ants.

Ant abundance, however, may be the primary trait affecting invasive ant-Homoptera mutualisms, as it may affect the interaction through several mechanisms. Higher ant numbers may translate into a higher probability of locating the tendees,

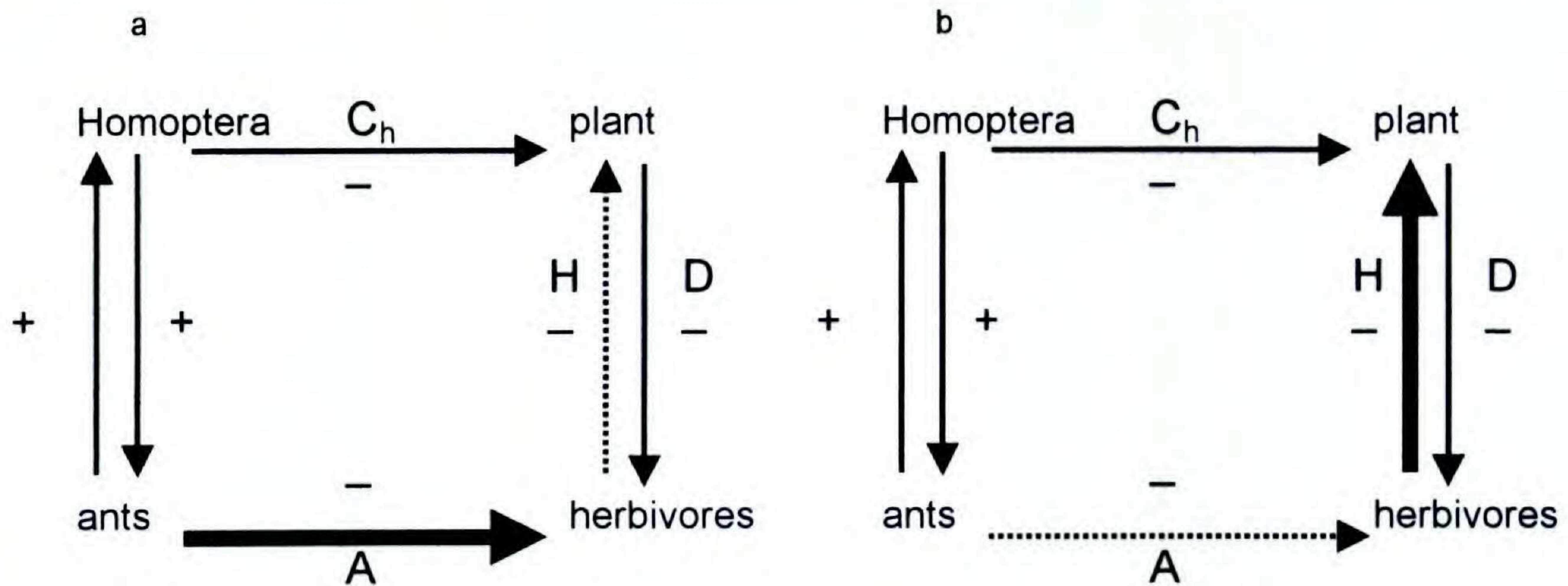


Figure 2. The ant-Homoptera mutualism when it results in a byproduct mutualism with the plant (2a) and when it is a parasite on the plant (2b). The direction of the arrows indicates the direction of the effect and the positive and negative signs show the type of effect. The thickness of the arrow indicates the strength of the effect. Dotted lines illustrate weak or no effect. C_h = the cost of hosting the Homoptera, H, A, and D are as defined in Figure 1. In 2a, the detrimental effect of the ants on the herbivores and subsequent decline in herbivore attack outweighs the cost to the plant of hosting the Homoptera. In 2b, the ants fail to deter herbivores so the plant bears the cost of hosting the Homoptera and attack by other herbivores.

and a higher ant:homopteran ratio may make ants more effective at deterring their partners' enemies (Steyn, 1955). Tending ants are a limiting resource to honeydew-producing Homoptera in many systems (Addicott, 1978; Sudd, 1987; Cushman & Addicott, 1989; Breton & Addicott, 1992; Fischer et al., 2001), and well-tended Homoptera may grow faster, reproduce more rapidly, and produce more young than untended ones (Way, 1963; Bristow, 1984; Morales, 2000). Where the ant:Homoptera ratio becomes too low, Homoptera may become ant prey or be more easily parasitized or preyed upon by natural enemies (Way, 1963, and references therein; Breton & Addicott, 1992; Sakata, 1994; Jolivet, 1996). The superabundance achieved by invasive ants may keep the tender:tendee ratio from falling below this threshold. In such a case, we would expect limits to the abundance of both mutualists to be imposed by the host plant.

Impacts on the plant, however, also may depend on whether the ants tending Homoptera deter other herbivores. In this byproduct mutualism (Yu, 2001), the plant benefits indirectly from the ants' presence; the ants benefit from the Homoptera hosted by the plant and possibly the herbivores, if they are captured as prey. In this scenario, Homoptera are analogous to extrafloral nectaries and Keeler's model (1981) can be modified as:

$$p[A(1 - D)H_{\text{non-Homoptera}}] > C_h$$

The right side of the equation (formerly the investment in nectar and nectaries, I_a) becomes the cost to the plant of hosting the Homoptera, C_h , including direct effects of lost phloem and indirect consequences such as mold accumulation and sus-

ceptibility to phytopathogens. Other terms remain the same: p = probability that ants will find the plant, A = effectiveness of ant-defense against (non-homopteran) herbivores, D = effectiveness of other defenses, H = intensity of (non-homopteran) herbivory. Considering the traits of invasive ants that favor high homopteran populations, it is probable that in many cases $C_{h\text{-invasive}}$ will be greater than $C_{h\text{-native}}$. The probability that the ant finds the plant, p , may vary not only with the abundance of the ant, but possibly with the ability of different Homoptera to recruit ants (Del-Claro & Oliveira, 1996). It is unclear, though, whether invasive ants may respond to attractant cues differently than native ants. Hypothesized differences in A , D , and H for native and invasive ants would be as explained above. As with the food-for-protection mutualism involving extrafloral nectaries, the byproduct mutualism will only be maintained if the benefits, in terms of deterred non-homopteran herbivores denoted on the left side of the equation, exceed the costs exacted on the plant by the Homoptera, the right side of the equation (Fig. 2a). If costs to the plant exceed benefits, the ant-Homoptera interaction will tend toward a parasitic relationship with its host (Fig. 2b), possibly resulting in reduced fitness of the plant. Studies that fail to detect any change in plant fitness with Homoptera outbreaks associated with invasive ants may be observing a balance between the two types of outcomes. As with interactions involving extrafloral nectaries, for invasive ants that are aggressive, abundant, and attracted to carbohydrate-rich resources, the model predicts maintenance of the byproduct mutualism if the potential

for herbivory is not diminished (i.e., through interactions away from the plant).

ANT IMPACTS ON PLANT REPRODUCTION

Seed set. With few exceptions (e.g., Yano, 1994; Puterbaugh, 1998), ants commonly have been regarded as unwanted guests in flowers (Kerner, 1878; Buckley, 1982). Attracted by floral nectar, ants may damage floral structures, and depress pollen viability with their antibiotic secretions (Kerner, 1878; Peakall et al., 1991; Galen, 1999). As with Homoptera and extrafloral nectary tending, superabundance and an affinity for carbohydrate resources combined with high levels of aggression would lead to the expectation that invasive ants would be exceptional at recruiting colony members to flowers and exploiting floral nectar.

If numerous aggressive ants are present in flowers, their presence may affect other floral visitors. Pollinators may be forced to reposition frequently to avoid attack by the ants, and this may result in increased transfer of pollen and consequently higher seed set. Alternatively, pollinators may avoid the flower altogether, or reposition too superficially for effective pollen transfer, ultimately resulting in decreased seed set (Wyatt, 1980). A plethora of floral antagonists, including pollen consumers, and other florivores, however, may also be deterred, perhaps compensating for any adverse effects on pollinators.

The ants' ultimate impacts on seed set will be dependent on the attraction and availability of floral nectar in the context of the ants' seasonal diet preferences, activity patterns, and abundance, the number of pollinators and floral antagonists and their susceptibility to ant deterrence, floral structure and defenses against ants, and the pollination requirements of the plant (Kerner, 1878; Koptur, 1979; Vinson & Greenberg, 1986; Huxley & Cutler, 1991; Klinkhamer & de Jong, 1993; Lanza et al., 1993; Koptur & Truong, 1998; Puterbaugh, 1998), as well as the relative difference between ants' effects on pollinators and floral antagonists. For example, I would expect nectar-robbing by invasive ants to have little effect on seed set across a plant population in an invaded area if there is little competition for the resource, e.g., if nectar is available in excess of demand by pollinators. I would expect invasive ants to be more likely to decrease seed set in a plant species that has few floral antagonists and is dependent on a few species of small pollinators, than in a species that suffers from many floral antagonists and has a diverse pollinator guild. Moreover, flowers in which nectaries are in close proximity to the stigma and anthers relative to the

ants' body size may be more affected by nectarivorous ants than those in which nectaries are farther away.

Seed predation and harvesting. Impacts of ants on seed dispersal and seed predation have received more attention than impacts on seed set. In myrmecochorous mutualisms, ants disperse seeds away from the parent plant, often burying them in their nest, in exchange for the lipid-rich eliasome attached to the seed (Buckley, 1982; Beattie, 1985). The dispersed seeds therefore may escape competition with siblings and parents and are less susceptible to predation and other threats, such as fire (Buckley, 1982; Beattie, 1985). Ants may also be seed harvesters, consuming the seed itself. Seed harvesters, however, do not eat all the seeds they collect, and therefore may act as accidental seed dispersers (Buckley, 1982; Hölldobler & Wilson, 1990).

Various species of ants may be attracted to eliasomes and opportunistically take part in myrmecochorous mutualisms, whereas harvester ants tend to have special adaptations for harvesting, consuming, and storing seeds (Hölldobler & Wilson, 1990; Keeler, 1989). In both cases, the ants need to (a) discover the seed, (b) recognize the seed as a resource, and (c) be able to carry the seed back to the nest. Seed discovery will be dictated by ant foraging patterns, seasonal and temporal overlap between ant activity and seed availability, and the attractiveness of the eliasome, if present (Beattie, 1985; Keeler, 1989). Seeds are typically high in lipids and proteins; recognition of the seed as a desirable resource may depend on the relative abundance and composition of other food sources in the environment and the dietary requirements of the colony when the seeds are available (Beattie, 1985). In every myrmecochorous system studied, seed-dispersing ants comprise only a small subset of the ant species present, and their behavior toward seeds can vary from one day to the next (Beattie, 1985), suggesting that recognition of the seed as a valuable food resource is not constant among ant species or over time for a single species. The ability to carry the seed back to the nest will depend on the ants' foraging behavior and size and shape complementarity between seed and ant (Keeler, 1989). Harvester ants must also have the mandibular strength and agility to ingest the seeds (Beattie, 1985).

How do we expect invasive ants to compare to native ants in these requirements? Traits of invasive ants that have formed the basis for hypotheses about other types of interactions discussed in this

paper, namely elevated abundance, aggression, and attraction to carbohydrates, may not have as much influence on seed predation and dispersal. Numerical superiority of invasive ants may increase the probability that they will discover seeds. However, common traits of invasive ants offer little capacity for predicting how invasive ants will respond to the seeds they encounter. Other traits that may be linked to seed discovery and dispersal may not vary consistently between invasive and native ants. *Solenopsis invicta* and *Pheidole megacephala* are attracted to oily, lipid-rich food sources (Vinson & Greenberg, 1986; Sanders et al., 1992), and seed harvesters occur in both genera (Hölldobler & Wilson, 1990). Thus, we might expect these invaders to be attracted to seeds, and even have some of the mandibular adaptations helpful for ingesting seeds, but perhaps no more so than native ants.

OTHER VARIABLES AFFECTING ANT-PLANT INTERACTIONS

As noted above, numerical superiority, aggressive behavior, and resource acquisition abilities of the ants are unlikely to account for all differences between invasive and native ant-plant interactions. Other biological traits that may vary substantially among ants, but are unlikely to vary consistently among invasive and native ants such as temperature tolerance, daily activity patterns, colony cycles, and seasonal preferences for food types will certainly affect ants' relationships with plants. Even for a single ant species, associations with plants may change spatially or temporally. For example, the degree of plant protection is largely linked to ant foraging patterns, which may change depending on the nutritional requirements of the colony (e.g., in relation to reproductive cycles), and the availability of carbohydrate and protein resources that require less foraging effort than those on the plant of interest (Ali & Reagan, 1985; Vinson & Greenberg, 1986; Stein et al., 1990; Rapp & Salum, 1995; Cornelius & Grace, 1997).

Attributes of the potential prey items, Homoptera, and the host plant will also play roles in defining ant interactions with these organisms (Way, 1963; Cushman, 1991; Huxley & Cutler, 1991; Bronstein, 1994), and invasive and native ants may diverge in their responses to these variables as well. Many herbivores (Van Der Goot, 1916; Kaak-eh & Dutcher, 1992; Pavis et al., 1992; Gunawardena & Bandumathie, 1993; Cornelius & Bernays, 1995; Montgomery & Wheeler, 2000; Brinkman et al., 2001) and flowers (Kerner, 1878; Willmer & Stone, 1997; Ghazoul, 2000) have effective chem-

ical or physical defenses against ants. Whether differences in ant size, recruitment ability, or tolerance to phytotoxins, for example, will enable certain groups of ants to evade these defenses is yet to be seen. In cases where herbivores and flowering plants have no evolutionary history with ants and therefore might lack specific defenses against ants (e.g., Hawai'i), invasive ants might not need to be especially aggressive or adept at thwarting defenses to deter herbivores or steal floral nectar.

TESTING THE PREDICTIONS WITH FIELD EVIDENCE

Do observations of invasive ant-plant interactions support predictions that the distinct combination of invasive ant traits will affect the outcome of their interactions with plants? Specifically, because of their combination of traits, are invasive ants more likely than native ants to deter herbivores, tend Homoptera to the detriment of host plants, and interfere with plant reproduction? There have been few direct tests. Most research on ant interactions with herbivores has been done in agroecosystems, has focused on how pest populations and crop yields are affected by changes in ant fauna, and has not explored any particular ant attributes influencing the interactions. Still less is known about how invasive ants affect seed set, predation, and dispersal. Nonetheless, examples below provide some evidence of the importance of the common traits of invasive ants while also underscoring the influence of ant biology and the role of other organisms in the system in determining the outcome of these interactions for the plant.

ANT PROTECTION FROM HERBIVORES

There are dozens of examples of invasive ants preying on or harassing would-be herbivores (see Holway et al., 2002, for a review). Almost none of these compare invasive to native ants, however, and rarely do they pinpoint any particular characteristic of the ant responsible for effects on herbivores. Some insights can be gained from cases in which the invader fails to deter herbivores. For example, *Anoplolepis gracilipes* affords protection from the sucking bug, *Amblypelta cocophaga* (China), in Solomon Islands coconut when it reaches high abundance in the trees. But when prey are abundant on the ground, *A. gracilipes* fails to forage in the trees and premature nutfall ensues due to *A. cocophaga* damage (Greenslade, 1971). In Keeler's (1981) terms, in this case a high A, ability to deter herbivores, is inconsequential if the probability of foraging on the plant (p) is low.

Extrafloral nectaries may serve to increase p.

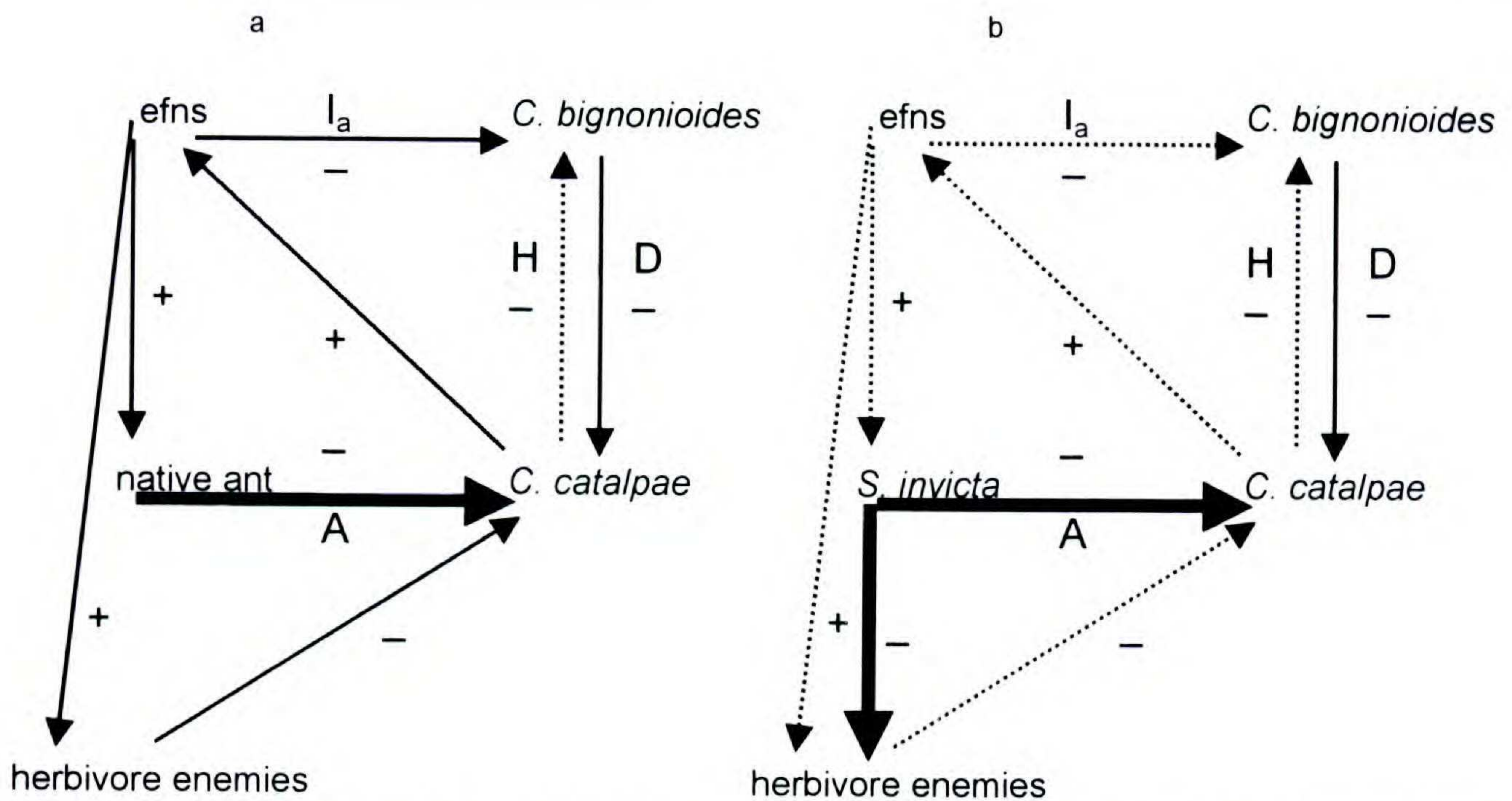


Figure 3. The food-for-protection mutualism between the tree *Catalpa bignonioides* and the dominant native ant (3a) and with *Solenopsis invicta* (3b). The direction of the arrows indicates the direction of the effect and the positive and negative signs show the type of effect. The thickness of the arrow indicates the strength of the effect. Dotted lines illustrate weak or no effect. I_a, H, A, and D are as described in Figure 1, efns = extrafloral nectaries. In 3a, the native ant and other enemies of the main herbivore, *Ceratoma catalpae*, are attracted to extrafloral nectar and are effective in reducing the herbivore attack on the plant. In 3b, *S. invicta* is not attracted to the extrafloral nectaries, deters *C. catalpae*'s other natural enemies, but still decreases the impact of the herbivore on the plant. In both scenarios, the extrafloral nectaries are induced by herbivory. See text for references.

Several studies have shown that different invasive ants are attracted to extrafloral nectar and can decrease herbivory on extrafloral nectar-bearing plants (see Holway et al., 2002, for a review). The high population density of *Pheidole megacephala* and its tending of extrafloral nectaries are blamed for the difference in populations of shrubs between *P. megacephala* and native ant-inhabited sites in Australian rainforest. The native *Urena lobata* L. and the introduced *Senna obtusifolia* (L.) H. S. Irwin & Barneby occur in dense stands and suffer little from folivory in areas invaded by *P. megacephala*, whereas in areas with native ants, the shrubs are small, isolated, and heavily attacked by herbivores (Hoffman et al., 1999). Other studies demonstrate that *Solenopsis invicta* (Fleet & Young, 2000), *Linepithema humile* (Koptur, 1979), and *Wasmannia auropunctata* (Meier, 1994) also are attracted to extrafloral nectaries on plants in their introduced habitats, sometimes to the benefit of the plant. But these studies, as with most, do not compare the behavior of invasive ants to that of native ants, nor do they explore specific attributes of invasive ants that may be influencing the interaction or its outcome.

Research exploring the interactions of *Solenopsis invicta* with *Catalpa bignonioides* Walter provides an interesting case study because it compares the

invasive to native ant's interactions with the tree and reveals specific attributes of the invader that are responsible for the differences. The production of extrafloral nectar is an inducible defense in this system; extrafloral nectar production increases in response to herbivory, thereby attracting native ants and parasitic wasps (Ness, 2001). Field experiments have shown that *S. invicta* displaces native ants and preys on the parasitic wasps of the predominant herbivore in the system, the caterpillar *Ceratoma catalpae* (Boisduval). Moreover, *S. invicta* visits extrafloral nectaries much less frequently than native ants, most likely due to peak extrafloral nectar production coinciding with the stage of colony cycle when workers prefer protein-rich resources. *Solenopsis invicta* is apparently as effective a predator of *C. catalpae* as are the native ants because it preys on pupae and pre-pupal instars as well as larvae, and because of its exceptional aggressiveness when prey are encountered. Thus, while *S. invicta* disrupts the mutualism by preventing other natural enemies of *C. catalpae* from visiting extrafloral nectaries and protecting *Catalpa bignonioides*, it does not do so at the cost of increased herbivory (Ness, 2001).

Putting the example in the context of Keeler's (1981) model (Fig. 3), even without the lure of extrafloral nectar, A_{Sinv} equals or exceeds A_{native} . $I_{a,Sinv}$

need not be as high as $I_{a \text{ native}}$; when *Solenopsis invicta* is present, neither the invasive ant nor the parasitic wasps visit the extrafloral nectaries as much as they are visited when native ants are present. In fact, because the extrafloral nectar is inducible, if *S. invicta* decreases the herbivore load more than native ants do, $I_{a \text{ Sinv}}$ will be lower than $I_{a \text{ native}}$. The difference between the benefits of reduced herbivory and the investment in extrafloral nectar production will be higher when *S. invicta* is present than when native ants are present.

It is worth noting that p , the probability of locating and foraging on the plant, may be influenced both by the abundance of the ant and its attraction to the nectar reward offered. As such, an extremely high density of *Solenopsis invicta* may offset its weak attraction to extrafloral nectar (Agnew et al., 1982). Indeed, high abundance of *S. invicta* has been offered as an explanation for the lack of any difference in its foraging frequency between nectaried and nectariless isolines of cotton (Agnew et al., 1982). Analogously, it is possible that high density of *S. invicta* in the invaded *Catalpa bignonioides* stand (Ness, 2001) facilitated the ants' foraging on the plant, notwithstanding the absence of its attraction to extrafloral nectar. In these cases, if abiotic or other conditions ever result in diminished abundance of *S. invicta*, the invader may become less effective at deterring herbivores than ants that may not be as abundant, but are lured to the plants by the nectar reward.

ANTS TENDING HOMOPTERA

Anoplolepis gracilipes, *Linepithema humile*, *Pheidole megacephala*, and *Wasmannia auropunctata* all have been noted for their ability to cause Homoptera outbreaks in various parts of the world (Holway et al., 2002). *Solenopsis invicta* may sometimes obtain carbohydrates directly from plant tissue (Vander Meer et al., 1995), but also has been associated with increased Homoptera populations (Lofgren, 1986; Holway et al., 2002). The data collected in these studies often fail to discern any particular trait of invasive versus native ants that are responsible for Homoptera outbreaks. While some evidence of the importance of abundance, aggression, and attraction to carbohydrate resources in invasive ant interactions with plants is seen in the examples below, evaluation of my prediction that these common invasive ant traits play a major role in determining their interactions with plants will be enhanced by further detailed study. However, some studies do allow us to examine the relative impact on the plant of the invasive ant as Homoptera ten-

der versus herbivore deterrent. These studies reveal that both types of outcomes outlined above occur, those in which the ant-Homoptera mutualism is parasitic toward the plant and those in which the ants tending Homoptera enter into a byproduct mutualism with the plant by deterring non-homopteran herbivores.

Linepithema humile's abundance, aggression, and tending of aphids have all been related to its ability to control populations of the pine processionary moth (*Thaumetopoea pityocampa* Den. & Schiff.) in Portugal pine plantations (Way et al., 1999). The aphids attract foraging *L. humile* to pine tree crowns. Later in the season, pine processionary moth larvae on trees with *L. humile* are fiercely attacked, whereas those on native ant-occupied trees are ignored. Consequently, parts of plantations that are inhabited by *L. humile* escape the severe defoliation caused by *T. pityocampa* in native ant-inhabited areas. Figures 4a and b contrast the interactions with the plant when native ants versus *L. humile* are present in terms of Keeler's (1981) modified model derived above.

Reviewing interactions of invasive ants and Homoptera in cacao (*Theobroma cacao* L.) is a study in contrasts, and illustrates the possibility for different outcomes to occur between the same plant and ant. In West Africa, *Wasmannia auropunctata* is actively spread among cacao plantations because it effectively deters pestiferous mirid bugs despite its association with high levels of scale and psyllids (Entwistle, 1972). In contrast, in its native Brazil, *W. auropunctata* tends the mealybug *Planococcus citri* (Risso) and many other Homoptera in cacao and fails to control pest herbivores possibly because it does not always achieve dominance in the ant mosaic (De Medeiros et al., 1995; De Souza et al., 1998). In the parlance of the modified Keeler (1981) model, in West Africa, C_h , the cost to the plant of hosting the Homoptera associated with *W. auropunctata*, is outweighed by the high A , the ability of *W. auropunctata* to deter key herbivores, and the ant can be said to have entered a byproduct mutualism with cacao. But in Brazil, *W. auropunctata* tending *P. citri* imposes a high C_h and a small A , resulting in a cost to the plant that exceeds the benefit.

Similarly, *Pheidole megacephala* in its native West Africa tends the mealybugs, *Planococcus citri* and *P. njalensis* (Laing), which are associated with swollen shoot virus in cacao (Taylor & Adedoyin, 1978; Campbell, 1994). As part of its tending behavior, *P. megacephala* transports soil from the ground to create tent shelters for the homopterans and thereby acts as a vertical vector of *Phytophtho-*

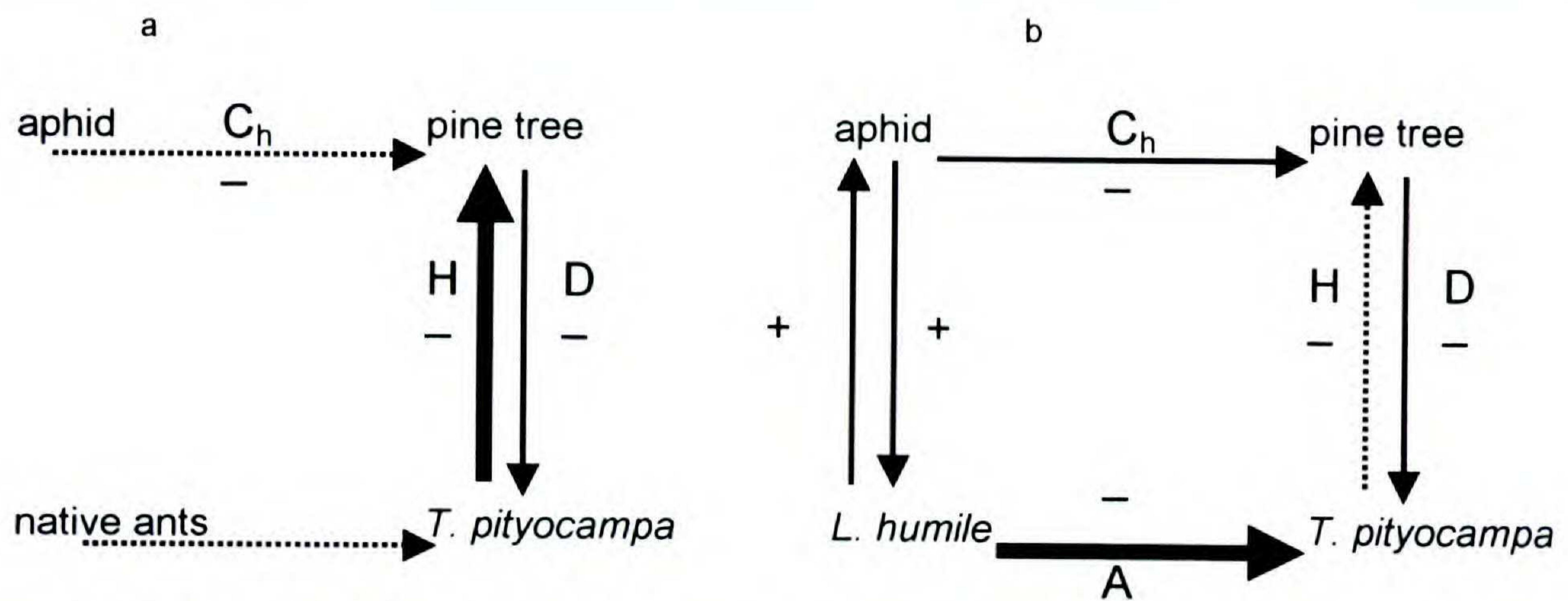


Figure 4. The native ant-*Thaumetopoea pityocampa*-pine tree relationship (4a) and the *Linepithema humile*-*T. pityocampa*-pine tree relationship (4b). The direction of the arrows indicates the direction of the effect and the positive and negative signs show the type of effect. The thickness of the arrow indicates the strength of the effect. Dotted lines illustrate weak or no effect. C_h , H, A, and D are as described in Figures 1 and 2. In 4a, the native ant is not attracted to the tree by aphids, fails to prey on the major herbivore, *T. pityocampa*, and the pine trees suffer from severe defoliation. Figure 4b illustrates the byproduct mutualism between *L. humile* and the pine tree. *Linepithema humile* is attracted to the trees by aphids and preys on *T. pityocampa* to the benefit of the plant. See text for references.

ra spores, the etiologic agent of black pod rot (Evans, 1973). In this case, C_h comprises not only the direct cost of hosting the mealybugs, but also the associated increased likelihood of being infected with two of the worst diseases of cacao. While no cacao studies have ever reported relationships between *P. megacephala* and non-homopteran herbivores, it is unlikely that strong deterrence of herbivores (a high A) would have gone unnoticed by farmers intimately aware of any effect on their yields. *Pheidole megacephala*'s frequent association with high Homoptera outbreaks to the detriment of plant fitness places it firmly in the pest category in West Africa (Taylor & Adedoyin, 1978).

In contrast, a low C_h and high A characterize the interaction between Homoptera, cacao, and *Anoplolepis gracilipes* in Papua New Guinea. The ant relies on honeydew-producing Homoptera to maintain its abundance (Baker, 1972). It displaces the native tent-building ants that facilitate transmission of black pod rot (Room & Smith, 1975; McGregor & Moxon, 1985; Way & Khoo, 1992). Moreover, unlike the ants it displaces, *A. gracilipes* harasses adult cocoa weevils and persistently disrupts egg laying and foraging of several mirid and coreid bugs, all of which are major pests (Entwistle, 1972; McGregor & Moxon, 1985; Way & Khoo, 1992). But the same ant fails to forage in trees in Malaysian cacao and so is not effective against herbivores (Way & Khoo, 1989), indicating that a low p , probability of finding and foraging on the plant, can undermine any ability to deter its herbivores.

The examples above suggest that ant-Homoptera mutualisms that are parasitic on the host plant are more likely to occur in the invaders' native range,

and those in which the mutualism benefits the plant may be more likely in the introduced range. If this were the case, we would expect that studies that report on invasive ant-Homoptera mutualisms but do not explicitly evaluate the effects of the ants on herbivores, would nonetheless observe improved plant fitness. But this is not the case; when plant fitness is noted, it is usually reported as decreasing (Beattie, 1985; Holway et al., 2002), suggesting that in most cases the invasive ant-Homoptera mutualism is parasitic for its host plant. Beattie (1985) further points out that the vast majority of data describing homopteran damage to plants is from agroecosystems, or other heavily manipulated environments where the population of natural enemies of Homoptera may be quite depauperate. Discerning whether there are differences in how the invasive ant-Homoptera mutualism affects plants in the ants' native versus introduced habitats and in agricultural versus less manipulated environments is worth additional research.

ANT IMPACTS ON PLANT REPRODUCTION

Even more so than with invasive ant interactions with extrafloral nectaries and Homoptera, the dearth of research into invasive ant impacts on seed set, seed dispersal, and seed predation precludes attempts to test the predictions outlined above at present. A brief review of the current state of knowledge can, however, point to early trends and identify areas for future research.

Although several species of invasive ants have been observed to forage in various flowers (Adams, 1986; Lofgren, 1986; Buys, 1990; Hara & Hata,

1992; Nicolson, 1994; Hata et al., 1995), little research has explored invasive ants' attraction to flowers and their interactions with pollinators. *Linepithema humile* is known to exploit floral nectar otherwise taken by bees (Buys, 1987), is associated with lower insect diversity in *Protea nitida* Mill. flowerheads (Visser et al., 1996), and is hypothesized to reduce seed set by deterring pollinators from some crops (Potgieter, 1937; Durr, 1952). But to date, no studies have been published that compare *L. humile*, or any other invasive ant, to native ants with respect to their attraction to flowers, interactions with floral visitors, and any subsequent impacts.

The impact of invasive ants on seed predation and dispersal has received a little more research attention. *Linepithema humile* in the South African fynbos is slower to discover eliasome-bearing seeds than the native ants that it displaces (Bond & Slingsby, 1984). Moreover, when the seeds are found, the invasive ants eat the eliasomes but fail to disperse and bury the seeds, leaving them vulnerable to predation and fire, and resulting in reduced seedling emergence in invaded sites (Bond & Slingsby, 1984). A recent experiment reported that the disruption of this myrmecochorous mutualism results in plant community changes (Christian, 2001), but this study did not take into account other potential effects of the ant on the plants (e.g., pollination) that also might have been responsible for the observed differences between invaded and uninvaded sites. In Corsica, *L. humile* is more likely to find and remove *Anchusa crisper* Viv. seeds with eliasomes than without, whereas the dominant native ants do not show a preference between seeds with and without eliasomes in the seeds they remove. It is unclear what impact the differences in behavior between the invasive and native ants may have on *A. crisper* population dynamics (Quilichini & Debussche, 2000).

Pheidole megacephala and *Solenopsis invicta* also appear to be attracted to seeds in their adopted habitats. *Pheidole megacephala* collects seeds of *Acacia concurrens* Pedley in Australia with unknown consequences for the tree (Majer, 1985). *Solenopsis invicta* is a predator of seeds of numerous crops and other plants (Ready & Vinson, 1995; Morrison et al., 1997) and is attracted to most eliasome-bearing seeds, but often destroys or scarifies them (Zettler et al., 2001). *Wasmannia auropunctata* is a poor seed disperser in its native Mexico (Horvitz & Schemske, 1986), but there are no published studies that examine its seed harvesting or dispersal tendencies in the habitats it has invaded. As with *Linepithema humile*, further study is nec-

essary to determine the impacts of *P. megacephala*, *S. invicta*, and *W. auropunctata* on seeds relative to native ants, and any implications for plant community dynamics.

WHY SHOULD WE STRIVE FOR PREDICTIVE CAPACITY?

The ability to predict the nature and outcomes of interactions between invasive ants and plants has the potential to yield many rewards. Agriculturalists and conservationists, in particular, may benefit by knowing whether a potential invader is likely to have impacts that will thwart their management goals. This foresight may provide further impetus for putting policies in place to prevent the invasion.

In cases where the invasive ant is already present, identification of the specific ant traits that influence the outcomes of invasive ant interactions with plants may reveal options for mitigating undesirable effects. If a key to many effects of invasive ants is their extreme abundance and penchant for carbohydrates, complete eradication from an area may not be necessary to prevent outcomes that are counter to land management goals. Agriculturalists have realized the link between invasive ants and Homoptera outbreaks, for example (Flanders, 1951; Prins et al., 1990; Reimer et al., 1990). Preventing the ants from foraging in trees via use of sticky barriers or other means decreases the Homoptera population below pest levels and deprives ants of this source of carbohydrates (Samways, 1990). Therefore, although the ants may still be present they no longer contribute to yield loss via their relationship with homopterans. Deprived of their carbohydrate source, they may not be abundant enough to effect other outcomes on the plants or native ant community (Addison & Samways, 2000).

Foraging conditions can also be manipulated naturally so that the ants are less pestiferous, or even aid in achieving management goals. In Zanzibar coconut, *Pheidole megacephala* is a pest because it does not prey on the primary agent causing premature nutfall, the bug *Pseudotheraptus wayi* (Brown), as much as the native weaver ant it displaces. *Pheidole megacephala* is attracted to the palm crown by nectar, pollen, and various homopterans. Retaining ground vegetation in palm plantations provides *P. megacephala* with enough foraging opportunity that it does not ascend the palm trees in search of food. The weaver ant is then free to inhabit the canopy and prey on *P. wayi* (Rapp & Salum, 1995). Similarly, in Louisiana sugar cane, allowing broadleaf weeds to grow in the early part

Table 2. Hypothesized contexts under which an individual plant may have a high or low risk of an adverse outcome or may benefit from association with an invasive ant for five types of ant-plant interactions.

	Protection from herbivores	Homoptera tending	Seed set	Seed dispersal	Seed predation
High risk of adverse outcome for plant	<p>Invasive ant: —is not attracted to plant, or —does not recognize herbivore as an enemy, and —displaces other ants that are effective protectors; and/or Herbivore: —is abundant, or —has defenses against ants; and Plant: —is lacking other effective defenses against herbivores</p>	<p>Invasive ant is: —present in high numbers, and and —seeking carbohydrates, and and —an effective deterrent of Homoptera natural enemies; and Homoptera: —produce honeydew, and —benefit from invasive ant tending; and Plant: —is vulnerable to Homoptera-associated phytopathogens or other effects of Homoptera abundance</p>	<p>Invasive ant is: —present in high numbers, and —seeking carbohydrates, and —attracted to the flower, and —an effective deterrent of pollinators; and Pollinators are: —not abundant, or —vulnerable to attack by aggressive ants; and Plant: —has no floral defenses against ants, and —has attractive nectar of medium availability, and —is pollen-limited</p>	<p>Invasive ant: —is not attracted to seeds and has completely displaced seed dispersing native ants, or —is attracted to seeds and is poor at seed handling and dispersing; and Plant: —is dependent on ants for seed dispersal</p>	<p>Invasive ant: —is attracted to seeds and is capable of damaging them; and Plant: —produces seeds without effective defenses against ant granivory, and —is seed-limited</p>
Low risk of adverse outcome for plant	<p>Invasive ant: —does not displace other ants that are effective protectors; and/or Herbivore is: —rare, or —vulnerable to ant attack; and/or Plant: —has other effective defenses against herbivores</p>	<p>Invasive ant: —has access to a carbohydrate source that is more attractive or requires less foraging effort, or —is not seeking carbohydrates, or drates, or —is not an effective deterrent of homopteran enemies; or Homoptera: —are not attractive to ants, or —do not increase with ant-tending</p>	<p>Invasive ant: —has access to a carbohydrate source that is more attractive or requires less foraging effort, or —is not seeking carbohydrates, or —does not deter pollinators from transferring pollen; or Pollinators are: —abundant and diverse, or —still able to transfer pollen in the presence of invasive ants; or Plant: —has broadly effective floral defenses against ants, or —has unpalatable or too little nectar to attract ants, or —produces copious nectar so that ants and pollinators do not compete, or —is not pollen-limited</p>	<p>Invasive ant: —is not attracted to seeds, and has not completely displaced seed-dispersing native ants, or Plant: —is not entirely dependent on ants for seed dispersal</p>	<p>Invasive ant is: —not attracted to seeds, or —not capable of damaging seeds; or Plant: —produces seeds with defenses against ant granivory, or —is not seed-limited</p>

Table 2. Continued.

	Protection from herbivores	Homoptera tending	Seed set	Seed dispersal	Seed predation
Potential for plant to benefit	<p>Invasive ant: —is highly attracted to plant, and —is effective at displacing herbivores</p>	<p>Invasive ant: —displaces other ants that are better Homoptera tenders; or —enters a byproduct mutualism with the plant (see text)</p>	<p>Invasive ant: —displaces other ants that are better nectar-robbers and pollinator deterrents, or —is seeking carbohydrates, and —is attracted to the flower, and —does not deter pollinators from transferring pollen; and Pollinators —transfer more pollen in the presence of the invasive ant (i.e., through increased repositioning frequency)</p>	<p>Invasive ant: —is attracted to seeds, and —is able to disperse and shelter them more effectively than any displaced ants</p>	<p>Invasive ant: —is not attracted to seeds, or —is not capable of damaging seeds; and —displaces other ants that are seed harvesters</p>

of the season facilitates an increase of *S. invicta* populations because it provides abundant prey (Ali et al., 1984). As the weeds die back with the closing of the sugarcane canopy, the ants transfer their foraging to the sugarcane where they are effective predators against the sugarcane borer, *Diatrea saccharalis* (F.) (Ali & Reagan, 1985).

SYNTHESIS AND CONCLUSIONS

Traits associated with invasive ants, namely elevated abundance, aggression, and attraction to high-carbohydrate resources directly and indirectly affect outcomes of interactions with plants. Abundance of invasive ants tends to be higher than native ants, but as shown in the examples, it is where, how, and when the bulk of these abundant workers tend to forage that ultimately influences interaction outcomes. As described above, while both *Anoplolepis gracilipes* and *Pheidole megacephala* can be abundant in coconut palm plantations, outcomes for coconut palms are quite different depending on whether conditions favor ground or arboreal foraging of the ants. However, the relative scarcity of *Solenopsis invicta* on *Catalpa bignonioides* appears not to be a factor in the protection of the plant from its main herbivore because it is offset by the ant's foraging efficiency. Invasive ant colony cycles and needs for a particular resource play a major role in determining foraging behavior, and may or may not coincide with plants' or Homoptera carbohydrate production and need for protection. In the case of *S. invicta* on *C. bignonioides*, had it been the time of year when *S. invicta* seeks carbohydrate-rich resources, or had the extrafloral nectar contained a profusion of amino acids, perhaps visitation frequency would have been higher and an even greater decline in herbivory witnessed (Ness, 2001). For host plants that suffer from a less palatable or vulnerable dominant herbivore or interact with a less aggressive ant, phenological overlap between ants' and plants' needs and rewards may be more critical to the outcome of the interaction (Bronstein, 1998).

The other invasive ant traits that I have focused on, aggression and attraction to carbohydrates, also deserve further examination. In predicting effects of invasive ants on plants, it will be useful to know what biochemical or other cues trigger the ants' aggressive behavior. Why, for example, does *Anoplolepis gracilipes* displace the coconut bug *Amblypelta cocophaga* in Solomon Islands coconut (Greenslade, 1971), but fail to deter the coconut bug *Pseudotheraptus wayi* in Zanzibar coconut (Way, 1953)? Likewise, carbohydrate resources can vary greatly in composition and therefore in their attraction of

ants. In any plant community, an ant may have the opportunity to choose among various floral nectars, extrafloral nectars, or homopteran exudates. The options and preferences may vary over the season and result in different outcomes for the individual plants and the plant community as a whole. For example, aphids attract *Solenopsis invicta* to nectaried cotton plants early in the season, but later in the season extrafloral nectar is preferred and the ants are seldom observed tending aphids (Agnew et al., 1982). The amount and types of amino acids and sugars, and the balance among them have all variously been suggested as affecting attraction of ants to nectar and homopteran exudates (Lanza, 1991; Lanza et al., 1993; Koptur, 1979; Vander Meer et al., 1995; Koptur & Truong, 1998). Further research may reveal whether invasive ants are attracted to certain carbohydrate sources more than native ants, and why an invasive ant may be more attracted to one carbohydrate source over another, as well as how any observed preferences change with other variables (e.g., availability of other resources, ant colony needs).

Elucidating the attractiveness and availability of different carbohydrate resources is likely the key to predicting when and where invasive ants will be found on plants and, therefore, the potential for a host of subsequent effects. Of the three attractants, Homoptera, extrafloral nectar, and floral nectar, it appears Homoptera are the most important lures for the invaders because of their near ubiquity and broad attractiveness to most invasive ants. Extrafloral nectar, while considered generally attractive to ants (Carroll & Janzen, 1973), is not as widely available. Moreover, plants that possess inducible extrafloral nectaries may offer nectar too inconsistently to appease the sweet tooth of invasive ants. Floral nectar is certainly common, but is perhaps not as universally attractive to ants unless floral defenses can be thwarted (Guerrant & Fiedler, 1981; Ghazoul, 2000). Once attracted to the plant, the invasive ant may deter herbivores, as part of the food-for-protection mutualism with extrafloral nectaries, or as part of a byproduct mutualism, an indirect effect of the ants' association with Homoptera. But an analogous byproduct parasitism, although not yet reported in the literature, is not implausible; invasive ants lured to plants by Homoptera or extrafloral nectaries may deter pollinators or a key herbivore enemy. Since evolution did not play a role in shaping the interactions between invasive ants and plants in their adopted habitats, we should not limit ourselves to considering only those outcomes that would be evolutionarily plausible.

That invasive ants can exert both positive and negative effects on plants precludes any generalization about the ultimate impact of invasive ants on plants. Indeed, the same ant may affect different parts and processes of the same plant in different ways at different times (Lofgren, 1986). Nonetheless, the existing data offer a starting point for predicting the context in which one outcome may be more likely than another for each type of interaction. In Table 2 I offer predictions about under what conditions an individual plant may face a high or low risk of an adverse effect or may benefit from association with an invasive ant for interactions involving plant protection, Homoptera tending, seed set, seed dispersal, and seed predation. A plant may simultaneously have a high risk of adverse outcomes in some categories and a low risk or potential to benefit in others. Net effects will depend on whether impacts combine or compensate for each other. For example, the reproductive capacity of a plant may be severely curtailed if an invasive ant both disrupts pollination and interferes with seed dispersal. Alternatively, there may be no net effect on a plant's reproductive success in the presence of an invasive ant that increases seed set and interferes with seed dispersal (e.g., Horvitz & Schemske, 1984). Plants may have their own compensatory mechanisms; angiosperms that rely on a few specialized pollinators may be clonal or extremely long-lived, thereby decreasing dependence on seed production (Bond, 1994).

The innumerable combinations of effects and vastly different potential net outcomes demonstrate the need for research that takes into account the multiple mechanisms through which invasive ants may affect plants, and the consequences for the plant at population and community levels. The complexity and context-dependency of ant-plant interactions make predicting the net effects of invasive ants on plants a formidable challenge. Nonetheless, incorporating characteristics common to invasive ants into pre-existing models of ant-plant interactions provides a framework for generating testable hypotheses about how invasive ants may interact with plants and the consequences for the plant. Testing these hypotheses will contribute directly to conservation and agriculture, and provide insights applicable to both invasion ecology and our understanding of ant-plant interactions.

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